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How striations of ophiuroid and asteroid trace fossils were produced—Observations of tube-feet movement in living ophiuroids and asteroids

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Abstract. To clarify the process of producing the striations in the trace fossil *Asteriacites*, we observed the behavior of living ophiuroids and asteroids in aquariums. When ophiuroids stopped crawling, they buried themselves shallowly in the substratum, removing substratum under their arms and discs by using their tube-feet. The basal-arm tube-feet produce well spaced, fine, parallel striations that are perpendicular to the arm axis. The oral tube-feet produce fine, radial striations in the central depression. When the ophiuroids resumed crawling, they raised their disc and four arms above the substratum and dragged one arm backward. The one backward arm erased the striations, and parallel fine striations remained in four arm depressions. Similarly, asteroids also produced wide and shallow striations perpendicular to the arm axis by tube-feet movement. When the asteroids started to move again, they bulldozed the substratum under the one preceding arm, where the striations were erased. Since the asteroids crawled raising the other four arms by their tube feet which produced rough and deep striations, the wide and shallow striations remained only in a half of each arm depression. The striations of *Asteriacites lumbricalis* and *A. quinquefolius* were similar in shape to the striations produced by movement of tube feet of living ophiuroids and asteroids, respectively.

Key words: *Asteriacites*, brittle star, sea star, striation, trace fossil, tube-foot

Introduction

Ichnospecies *Asteriacites lumbricalis* Schlotheim, 1820 and *A. quinquefolius* (Quenstedt, 1876) are well known star-shaped trace fossils. In previous studies, these two ichnospecies have been distinguished by the following features. *Asteriacites lumbricalis* has a distinct central subcircular area with narrow arms and faint striations in the arms (Seilacher, 1953; Hakes, 1976; Twitchett and Wignall, 1996; Ishida *et al*., 2004), and *A. quinquefolius* has wide arms from an undifferentiated center and dense striations in the arms (Seilacher, 1953; Patel *et al*., 2008; Ishida *et al*., 2013).

The producers and their producing processes have been studied based mainly on the shape of traces (e.g. Seilacher, 1953; Mángano *et al*., 1999; Ishida *et al*., 2004, 2013). However, the detailed morphology of the traces including striations (bioglyphs; Seilacher, 2007) and how the traces are produced have not been clarified well enough. For the paleontological implications of trace fossils, to specify the producing organisms and to clarify the producing processes are the most important, and observations of morphology and behavior of living organisms are effective methods to interpret trace fossils. *Asteriacites lumbricalis* was interpreted as a resting trace of ophiuroids (Seilacher, 1953; Chamberlain, 1971; Mikuláš, 1990; West and Ward, 1990; Mángano *et al.,* 1999; Wilson and Rigby, 2000; Ishida *et al.,* 2004, 2013), while *A. quinquefolius*

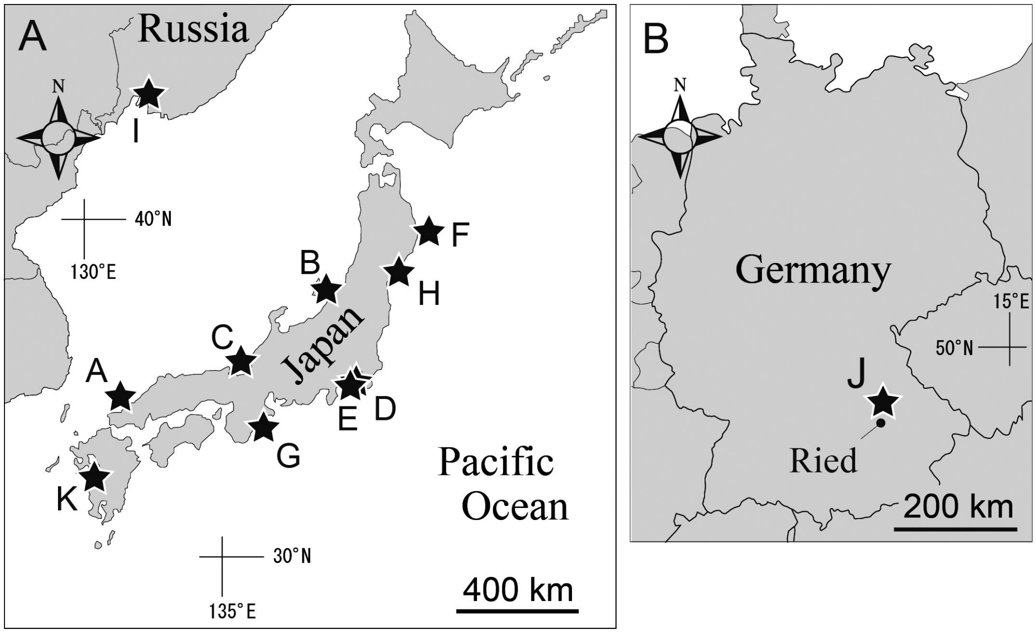

Figure 1. Sampling localities in Japan and Russia (**A**) and Germany (**B**). Star-shaped symbols indicate sampling localities, and letters near the symbols denote the site number.

was interpreted as a resting trace of asteroids (Seilacher, 1953; Patel *et al*., 2008; Ishida *et al.*, 2013).

Both named fossils have characteristic striations on their arms. Seilacher (1953, 2007) observed the traces produced by living ophiuroids and asteroids in an aquarium and suggested the striations were marked by tube-feet, but morphological details of the striations and the behavior of the ophiuroids and asteroids producing them have never been studied. In the present study, we observed the tube-feet movement and the striations produced by living ophiuroids and asteroids in an aquarium as well as *in situ*. We compared their striations with those of *Asteriacites lumbricalis* and *A. quinquefolius* from four formations, and the producers of these trace fossils were precisely specified. In addition, the morphologies of striations of previously reported *Asteriacites* fossils were reconsidered based on our observations.

Material and methods

Two extant ophiuroid species *Ophiura kinbergi* (Ljungman, 1866) and *Stegophiura sterea* (H. L. Clark, 1908) and one extant asteroid species *Astropecten scoparius* Müller and Troschel, 1842 were used for the laboratory observations. For *O. kinbergi*, six specimens (7.9–8.9 mm in disc diameter) were recovered at a depth of 80 m in the Sea of Japan (Site A in Figure 1A) during the research cruise of T. S. *Toyoshio-maru* of Hiroshima University in July 2001 and four specimens (2.5–3.9 mm in disc diameter) were recovered at a depth of 6–15 m in May 2012 in Tateyama Bay, Japan (Site D in Figure 1A), by the research boat *Sea-star* of Ochanomizu University. One specimen (6.6 mm in disc diameter) of *S. sterea* was recovered at a depth of 200 m in the Sea of Japan (Site B in Figure 1A) during the research cruise of R. V. *Mizuho-maru* of the Japan Sea National Fisheries Research Institute in May 2002. For *A. scoparius*, one specimen (72 mm in arm length) was recovered at a depth of 45–49 m in Manazuru Bay, Japan (Site C in Figure 1A) during the research cruise of R. V. *Ryokuyo-maru* of the Field Science Education and Research Center, Kyoto University in March 2012, and one specimen (115 mm in arm length) was recovered from a depth of 6–15 m in May 2012 in Tateyama Bay (Site D in Figure 1A), by the research boat *Sea-star* of Ochanomizu University. Additionally, one specimen (32 mm in arm length) was collected by hand from the intertidal zone in Aburatsubo Bay, Japan (Site E in Figure 1A) in August 2012.

The animals were kept alive in laboratories before observation. Behavior of one individual of *Stegophiura sterea*, eight individuals of *Ophiura kinbergi* and two individuals of *Astropecten scoparius* in a glass beaker (17 cm in diameter and 9.5 cm in height) or that of two individuals of *O. kinbergi* and one individual of *A. scoparius* in a plastic tray (30 × 22 × 5 cm in size) was observed at room temperature (12–25˚C). Two different kinds of substratum were filled in to a thickness of 10 mm: beach sand (0.2–0.5 mm in grain size equivalent to fine to medium

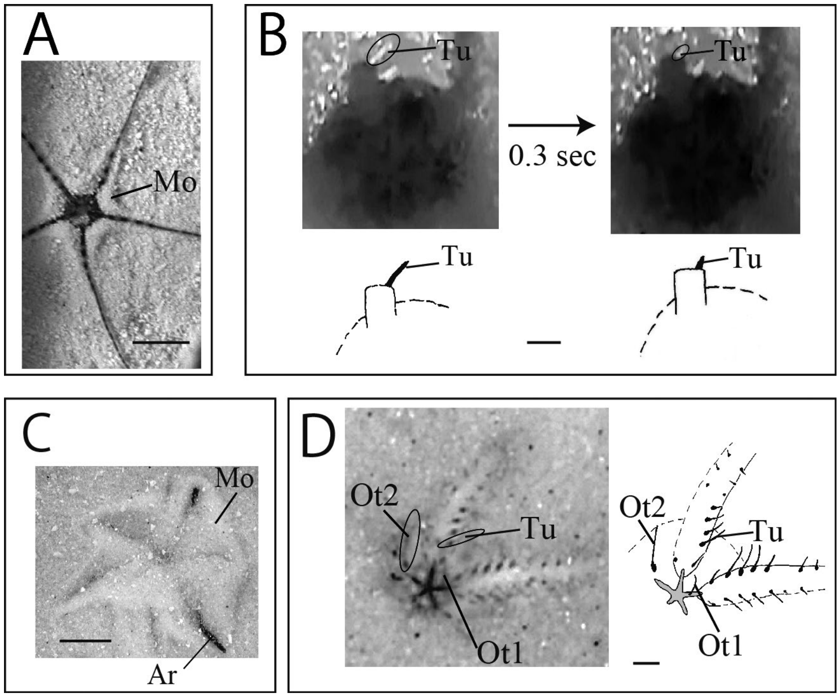

Figure 2. Tube-feet movement of extant ophiuroids, *Ophiura kinbergi* (A, B) and *Stegophiura sterea* (C, D), when burrowing into beach sand observed in the glass beaker. Video images and sketches of them are shown in B and D. **A**, resting posture, upside view, specimen from Site A. **B**, successive underside images when burrowing (time interval 0.3 sec), specimen from Site D. A basal-arm tube-foot is extended and retracted. **C**, resting posture, upside view, specimen from Site B. **D**, underside image when burrowing, specimen from Site B. Most of basal-arm tube-feet and oral tube-feet are extended. Abbreviations: Ar, arm; Mo, mound of substratum; Ot1, first oral tube-foot; Ot2, second oral tube-foot; Tu, tube-foot. Scale bars equal 5 mm (A, C) and 1 mm (B, D).

sand) in a glass beaker and aluminiferous abrasive (#1500 in grain size equivalent to mud) in a plastic tray. Tube-feet movement of the ophiuroids and asteroids was recorded by a video camera from the under and lateral sides of the glass beaker. Their traces that remained on the surface of the substratum were photographed from above the water surface. Sizes of oral and basal-arm tube-feet of one individual of *O. kinbergi*, one individual of *S. sterea* and of tube-feet of one individual of *A. scoparius* were measured on the video by a caliper square.

Star-shaped traces on the sea bottom produced by the living ophiuroid and asteroid were reported on photographs of the deep-sea floor in Japan (Ishida *et al.*, 2004, 2013). The trace of the ophiuroid *Amphiophiura penichra* (H. L. Clark, 1911) was taken on the silt bottom at 730 m deep off northern Japan in July 1984 (Site F in Figure 1A) and that of an astropectinid asteroid on the silt bottom at 861–923 m deep off central Japan in May 1986 (Site G in Figure 1A), by a deep-sea camera during cruises of R. V. *Tansei-maru* of the Ocean Research Institute, University of Tokyo. Striated traces were observed in the star-shaped traces in the underwater photographs.

Three *Asteriacites* fossils already reported in previous papers from two formations were reexamined, in particular, with respect to their striations: a concave epirelief of *Asteriacites lumbricalis* (diameter of central depression 13.2 mm, depth of central depression 0.5 mm, arm length 22.1 mm) in the mudstone of the Olenekian (Lower Triassic) Hiraiso Formation in Miyagi Prefecture, Japan (Site H in Figure 1A) (Kamada and Takizawa, 1992; Ishida *et al.*, 2004); a concave epirelief of *A. lumbricalis* (diameter of central depression 7.7 mm, depth of central depression 0.3 mm, arm length 23.4 mm) in the fine-grained limestone of the lower Tithonian (Upper Jurassic) Hienheim Formation at Ried, Germany (Site J in Figure 1B) (Röper and Rothgaenger, 1995, 1998; Ishida *et al.*, 2013); a concave epirelief of *A. quinquefolius* (depth of central depression 5 mm, arm length 53 mm) in the fine-grained limestone of the lower Tithonian (Upper Jurassic) Hienheim Formation at Ried, Germany (Site J in Figure 1B) (Röper and Rothgaenger, 1995, 1998; Ishida *et al.*, 2013). Additionally, two unidentified star-shaped trace fossils from two formations were also examined: a convex hyporelief (diameter of central ridge 7.1 mm, height of central ridge 0.5 mm, arm length 16.9 mm) in the medium sandstone of the Spathian (Lower Triassic) Lazurnaya Bay

Table 1. Measurements of tube-feet and space between them of *Ophiura kinbergi* (disc diameter 3.9 mm), *Stegophiura sterea* (disc diameter 6.6 mm) and *Astropecten scoparius* (arm length 115 mm). Mean and range are shown for basal-arm tube-feet. Length and width were measured when extended during burying into the substratum.

Species	First oral tube-feet (*n* = 1)			Second oral tube-feet (*n* = 1)			Basal-arm tube-feet (*n* = 4)			
	Length (mm)	Width (mm)	Width/ Length	Length (mm)	Width (mm)	Width/ Length	Length (mm)	Width (mm)	Width/ Length	Space (mm)
Ophiura kinbergi	0.90	0.19	0.22	1.05	0.21	0.20	0.63 (0.59–0.65)	0.13 (0.16–0.21)	0.21 (0.10–0.12)	0.46 (0.46–0.46)
Stegophiura sterea	1.98	0.19	0.10	2.16	0.25	0.12	1.69 (1.61–1.80)	0.18 (0.16–0.21)	0.11 (0.11–0.12)	0.61 (0.61–0.61)
Astropecten scoparius	–	–	–	–	–	–	13.9 (13.3–15.0)	4.3 (4.0–4.9)	0.32 (0.30–0.33)	0 (0–0)

Formation on Russky Island, South Primorye, Russia (Site I in Figure 1A) (Shigeta *et al.*, 2009); a concave epirelief (diameter of central depression 34.4 mm, depth of central depression 4.0 mm, arm length 39.0 mm) in the fine sandstone of the Upper Cretaceous Himenoura Group on Makishima Island in Kumamoto Prefecture, Japan (Site K in Figure 1A) (Komatsu *et al.,* 2008; Kojo *et al.*, 2011). The striations of the ichnofossils were observed using a binocular microscope or by tracing them onto transparent paper placed upon the fossil-bearing sediment.

The trace fossil specimens from the Hienheim Formation are housed at the Bürgermeister-Müller-Museum, Solnhofen, Germany (BMMS). The specimens from the Hiraiso Formation and Lazurnaya Bay Formation and the synthetic resin cast from the Himenoura Group are housed at the National Museum of Nature and Science, Tsukuba, Japan (NMNS PA 18300, 18301, 18302, respectively).

Results

Aquarium observations of extant species

In the aquarium, the ophiuroids *Ophiura kinbergi* and *Stegophiura sterea* usually crawled on the substratum or sat on it with their body shallowly buried. When they sat, *Ophiura kinbergi* buried itself more shallowly than *S. sterea* (Figure 2A, C). Both ophiuroids sat by burying the disc and basal arms into the sediment and thereby small mounds of the sediment were formed around the discs and along the basal arms (Figure 2A, C). They dug down into the substratum by mainly using basal-arm tube-feet and oral tube-feet (Figure 2B, D). Basal-arm tube-feet were slender and widely apart (Table 1). The ophiuroids repeated the motion of extending basal-arm tube-feet outward and retracting them inward to sweep away the substratum under the arms (Figure 2B). One extension and retraction of the basal-arm tube-feet took about 0.5 second for *O. kinbergi* and 2.0 seconds for *S. sterea*. On the other hand, longer first and second oral tube-feet in discs (Table 1) moved cyclically in a radial direction to sweep away the substratum under the disc (Figure 2D). One cycle of this movement of the first and second oral tube-feet took about 0.9 and 1.3 seconds for *O. kinbergi* and 2.2 and 3.3 seconds for *S. sterea,* respectively. The substratum swept away by basal-arm tube-feet and oral tube-feet formed mounds at the side of the body (Figures 2A, C, 3A).

When the ophiuroids started to emerge again from the substratum, they raised rapidly their disc and the basal parts of four arms above the substratum, and moved pushing the substratum with the distal parts of the four arms, dragging the remaining arm backward. Consequently, a disc and four-arm trace was formed (see also Ishida *et al.*, 2004 for production of resting traces of ophiuroids). The striations remaining in the resting trace were fine, spaced corresponding to the space between neighboring basal arm tube-feet, parallel to each other and perpendicular to the arm axis in the basal "arms." Fine and radial striations remained in the central depression (Figure 3).

The asteroid *Astropecten scoparius* usually moved on the substratum or sat with its body shallowly buried in it. When the asteroid sat, it buried its arms into the sediment and small mounds of the sediment were formed along the arms. It dug down into the substratum by mainly using thick basal-arm tube-feet (Table 1). The tube-feet showed a cyclic movement, extending outward and retracting inward, to sweep away the substratum under the arms (Figure 4A). The tube-feet were very close or in contact with each other (Figure 4A, Table 1). One cycle of this movement was about 5 seconds. The sediment swept away by tube-feet formed mounds (Figure 5A). The asteroid moved with one preceding arm and four arms extended in a lateral direction (Figure 5A). So, under the four lateral arms, tube-feet moved perpendicularly

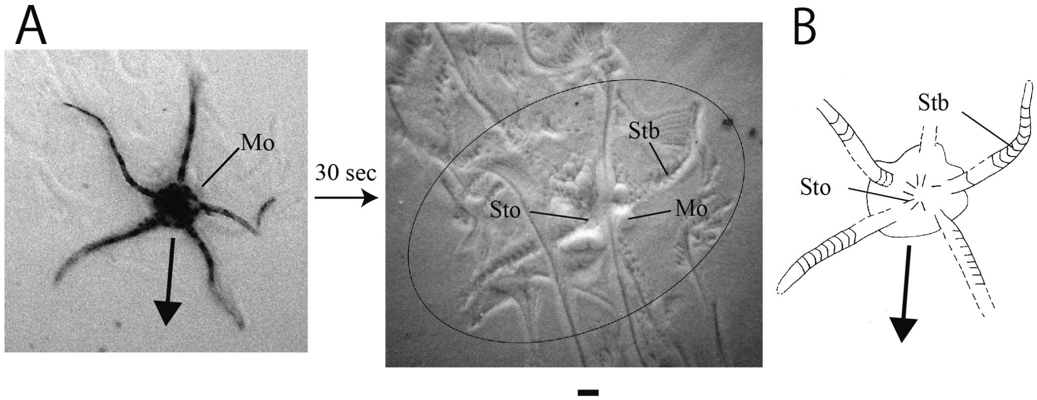

Figure 3. Producing process of striations on aluminiferous abrasive by *Ophiura kinbergi* (specimen from Site D), observed in the plastic tray. **A**, successive images when starting to move again from its resting posture (time interval 30 sec). One conspicuous trace marked by an oval was produced after the ophiuroid moved. **B**, sketch of striations of the conspicuous trace. Arrows indicate the direction which the ophiuroid moved. Abbreviations: Mo, mound of substratum; Stb, striation by basal-arm tube-feet; Sto, striation by oral tube-feet. Scale bar equals 1 mm.

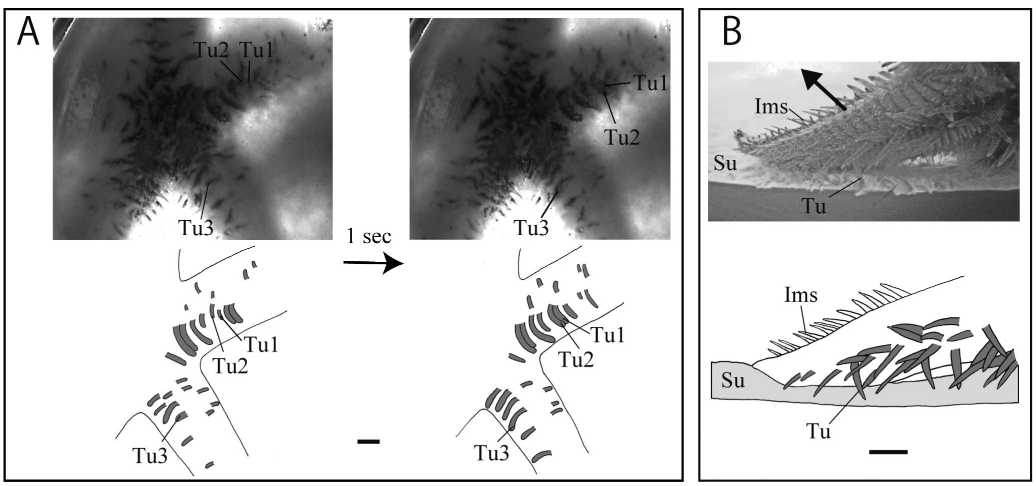

Figure 4. Tube-feet movement of *Astropecten scoparius* when burrowing and starting to move again observed on beach sand in the glass beaker. Video images and sketches of them are shown in A and B. **A**, Successive underside images when burrowing (time interval 1 sec), specimen from Site D. Tube-feet were extended and retracted. **B**, lateral image when starting to move again, specimen from Site E. Tube-feet were stuck into the sediment. Arrows show the direction in which the asteroid moved. Abbreviations: Ims, infero-marginal spine; Su, substratum; Tu1–3, tube-foot, identical tube-feet are shown by the same numbers. Scale bars equal 1 cm.

to the arm axis (Figure 4A). When the asteroid started to shift again, it bulldozed the substratum under the one preceding arm, and the depression of the arm was completely destroyed. However, the other four depressions remained (see also Ishida *et al.,* 2013). The tube-feet were stuck deeply into the sediment in the front half of four arm depressions (Figure 4B), and the deep and irregular striations were redrawn there (Figure 5B). On the other hand, in their back half, wide and parallel striations contacting with each other, originally formed when digging, remained (Figure 5B).

In the basal part of the arm depressions of traces, the striations of both ophiuroids and asteroids were parallel to each other and perpendicular to the arm axis, but the striation width was different between them. Moreover, ophiuroid traces had radial striations in the center of the depression (Figures 3, 5).

In situ observations of extant species

Striations in the star-shaped traces made by the ophiuroid *Amphiophiura penichra* were clearly visible in the four arm depressions, and they were well spaced, fine, parallel to each other and perpendicular to the arm axis (Figure 6). Fine radial striations were also found in the center of the depression (Figure 6). These striations were very similar to those of *Ophiura kinbergi* in the aquarium

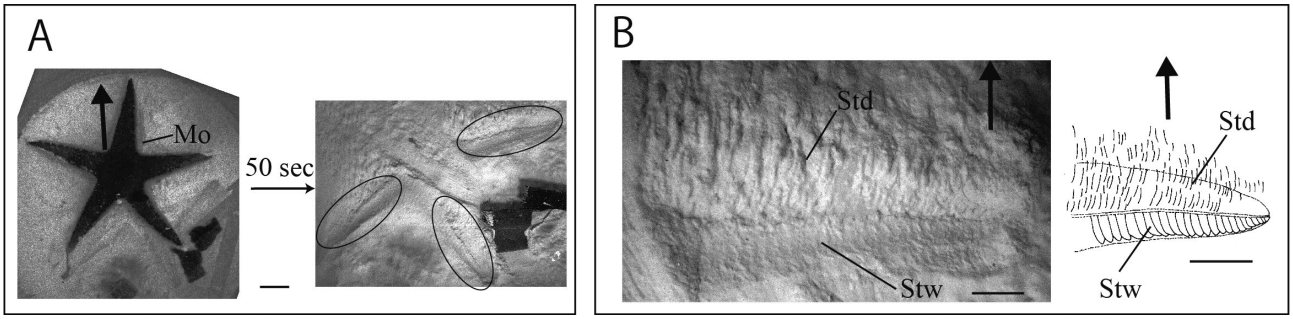

Figure 5. Producing process of striations on aluminiferous abrasive by *Astropecten scoparius* (specimen from Site C) observed in the plastic tray. **A**, successive images when starting to move again from its resting posture (time interval 50 sec). Three arm depressions marked by ovals were produced after the asteroid moved. **B**, enlarged view of the striations and sketch of a part of it. Arrows show the direction in which the asteroid moved. Abbreviations: Mo, mound of substratum; Std, deep striation; Stw, wide striation. Scale bars equal 1 cm.

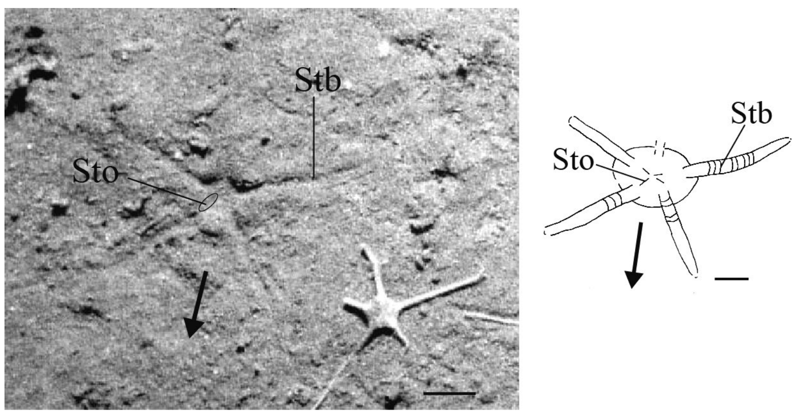

Figure 6. Striations in a star-shaped trace produced by the ophiuroid *Amphiophiura penichra* on the deep-sea floor (Site F). A star-shaped trace on the left photograph is sketched at right. Arrows show the estimated direction in which the ophiuroid moved. Striations are observed in arm depressions and in a central depression (marked by an oval). The bottom sediment is silt. Abbreviations: Stb, striation by basal-arm tube-feet, Sto, striation by oral tube-feet. Scale bars equal 1 cm. Modified from Figure 5B in Ishida *et al.* (2004).

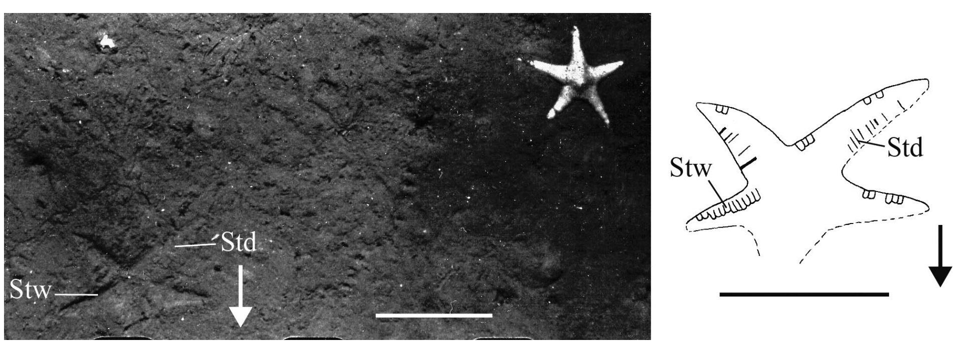

Figure 7. Striations in a star-shaped trace produced by an astropectinid asteroid on the deep-sea floor (Site G). A star-shaped trace on the left photograph is sketched at right. Arrows show the estimated direction in which the asteroid moved. The bottom sediment is silt. Abbreviations: Std, deep striation; Stw, wide striation. Scale bars equal 5 cm. Modified from Figure 5G in Ishida *et al.* (2013).

observation.

Striations of an astropectinid asteroid were found in the four arm depressions, and they were perpendicular to the arm axis (Figure 7). In each arm depression, in one half the striations were wide, regular, and in contact with each other, while in the other half they were deep and irregular (Figure 7). The striations are similar to those of *Astropecten scoparius* in the aquarium observation.

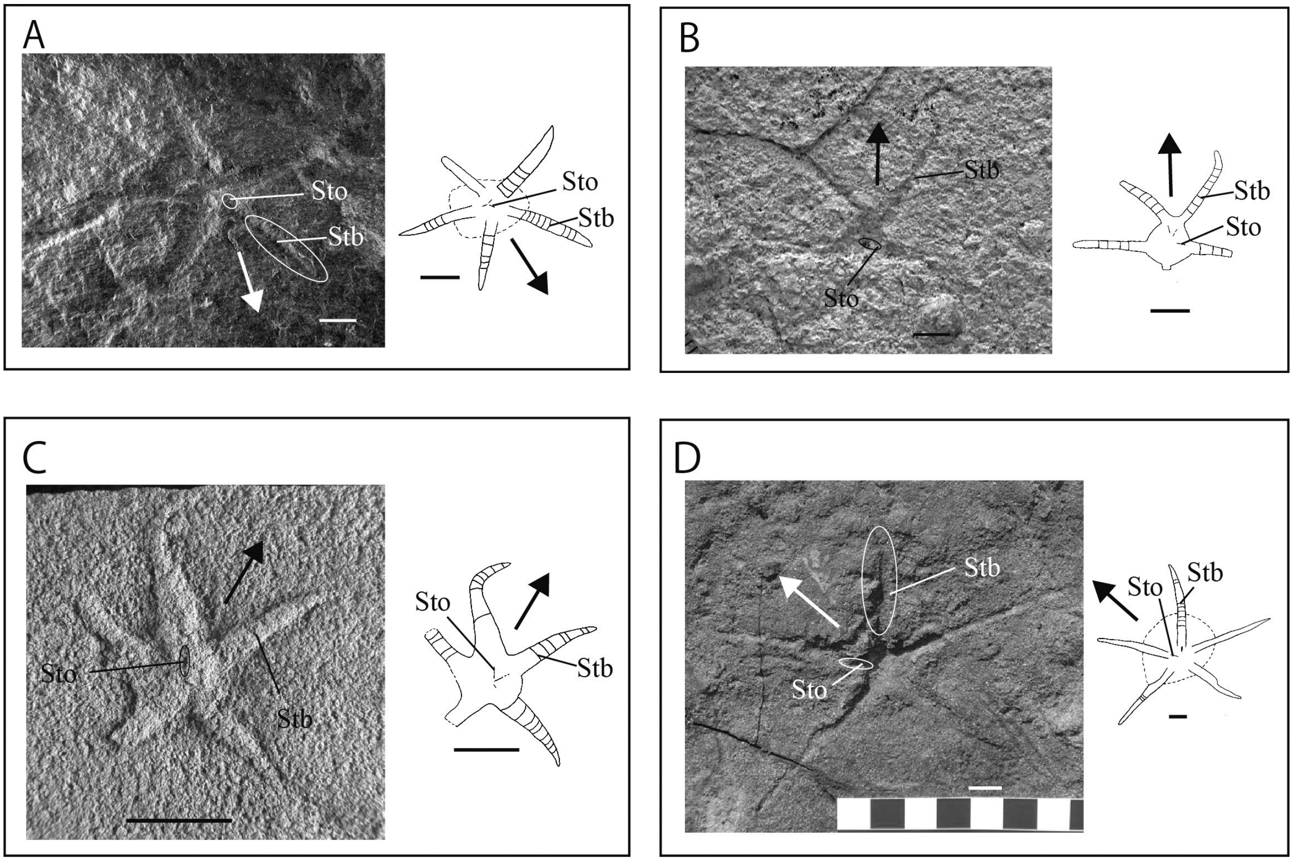

Figure 8. Striations of trace fossils of *Asteriacites lumbricalis*. Traces on the left photographs are sketched at right. **A**, Triassic Hiraiso Formation, mudstone (NMNS PA 18300, modified from Ishida *et al.*, 2004, fig. 3); **B**, Jurassic Hienheim Formation, fine grained limestone (BMMS); **C**, Triassic Lazurnaya Bay Formation, medium sandstone (NMNS PA 18301); **D**, Cretaceous Himenoura Group, fine sandstone (NMNS PA 18302, synthetic resin cast of this material). Arrows show the direction of travel of the ophiuroids that produced these traces. Striations are marked by ovals. Abbreviations: Stb, striation by basal-arm tube-feet; Sto, striation by oral tube-feet. Scale bars equal 5 mm (A, B, C) and 1 cm (D).

Trace fossils

The trace fossils of *Asteriacites lumbricalis* from the Lower Triassic Hiraiso Formation (Figure 8A) and the lower Tithonian (Upper Jurassic) Hienheim Formation (Figure 8B) had fine, well spaced striations, parallel to each other, and perpendicular to the arm axis in four arm depressions, and faint, radial, fine striations in the center depression. Star-shaped trace fossils from the Triassic Lazurnaya Bay Formation (Figure 8C) and the Cretaceous Himenoura Group (Figure 8D) were identified also as *A. lumbricalis* by having a small form, a central disc and relatively narrow arms. They also had fine, well spaced striations, parallel to each other and perpendicular to the arm axis, and radially fine striations. The striations of these fossils were similar to those of the resting trace of living ophiuroids.

The trace fossils of *Asteriacites quinquefolius* from the Upper Jurassic Hienheim Formation (Figure 9) had both wide, regular and contact striations and deep and irregular striations in the arm depressions. The striations were similar to those of the resting trace of living asteroids in shape, direction and location.

Discussion

The detailed morphology of striations and their producing process were clarified in this study. Similar striations to those of this study were found also in the trace fossils reported in previous papers. Striations similar to those of resting traces of extant ophiuroids were observed in *Asteriacites lumbricalis,* from the Lower Devonian of the Union of South Africa (Fourie, 2009, figure on p. 33), from the upper Carboniferous of U. S. A. (Hakes, 1976, pl. 1, fig. 1c), from the Lower Triassic of U. S. A. (Wilson and Rigby, 2000, fig. 3) and from the Lower Jurassic of Germany (Seilacher, 1953, fig. 1). Moreover, *Asteriacites* sp. from the Carboniferous of U. S. A. (Hakes, 1976, *loc. cit.*) and an unidentified star-shaped trace fossil from the

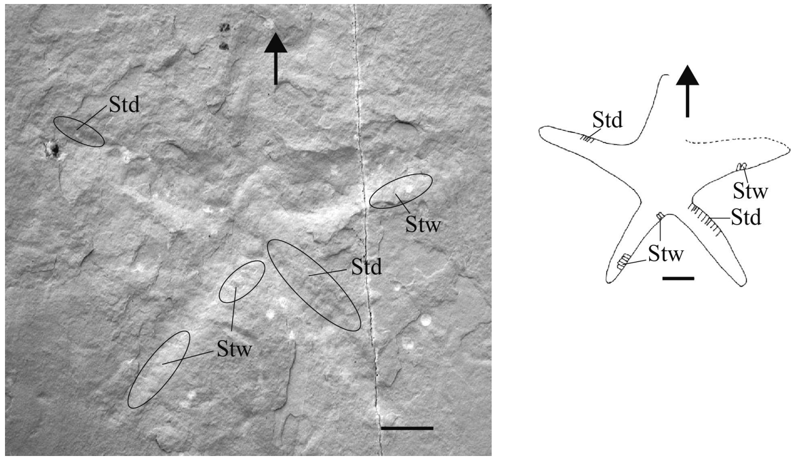

Figure 9. Striations of trace fossils of *Asteriacites quinquefolius*, Jurassic Hienheim Formation, fine-grained limestone (BMMS). A trace on the left photograph is sketched at right. Arrows show the direction of travel of the asteroid that produced the resting trace. Striations are marked by ovals. Abbreviations: Std, deep striation; Stw, wide striation. Scale bars equal 1 cm. Modified from Ishida *et al.* (2013, fig. 3).

Upper Jurassic of Germany (Röper and Rothgaenger, 1998, fig. 135) were probably *A. lumbricalis* due to their small form with slender arm depressions, a central subcircular depression and the strikingly similar striations. Striations similar to those of resting traces of extant asteroids were also found in *A. quinquefolius* from the Middle Jurassic of Switzerland (Seilacher, 1953, table 10, fig. 2). The star-shaped trace fossil from the Upper Jurassic of Germany (Röper and Rothgaenger, 1998, fig. 146) was probably *A. quinquefolius* due to its large form with the wide arm depressions and the typical striations.

Seilacher (1953) suggested that the striations of *Asteriacites lumbricalis* and *A. quinquefolius* were marked by tube-feet of ophiuroids and asteroids, respectively, by comparing the shape of striations remaining on the substrate in aquarium observations, but he did not observe the tube-feet movement. In his observations, striations made by ophiuroids were parallel to each other in the arm depressions and radial in the central depression, whereas striations made by asteroids were irregular in the arm depressions, and the morphological details of the striations were not made clear (Seilacher, 1953). In this study, the movement of tube-feet to produce the striations and the morphology of the striations produced by the movement were observed in detail using extant animals in an aquarium for the first time. Additionally, striations were observed on *in situ* photographs of star-shaped traces on the sea floor. Based on these observations, we showed that the morphology of striations was completely different between *A. lumbricalis* and *A. quinquefolius*, and that these different striations were produced by different producers, ophiuroids and asteroids, by the different morphology and behavior of the tube-feet.

When ophiuroids buried themselves, not only basal-arm tube-feet but also oral tube-feet were used for sweeping away the substratum under their body (Figure 10A, 1). This behavior of oral tube-feet digging in the substratum has never been reported. The oral tube-feet behavior when burrowing into the substratum was recently observed also in a possibly infaunal species of Ophiomycetidae (Masanori Okanishi *et al*., unpublished data).

The striations in the resting traces of ophiuroids and asteroids found on the deep-sea floor agreed with the striations of those in aquariums morphologically (Figures 6, 7), but some differences were recognized. The striations made by ophiuroids on the silty deep-sea floor (Figure 6) were fainter than those in the aquarium (Figure 3) and the asteroids' deep irregular striations in the front half of arm depressions on the silty deep-sea floor (Figure 7) were deeper than those in the aquarium (Figure 5), probably because the substratum is finer on the deep-sea floor than in the aquarium. Similar striation morphology of ophiuroids and asteroids were observed both in the aquarium and on the sea floor, thus strengthening the identification of the producers of the trace fossil *Asteriacites*.

In previous studies, two ichnospecies of *Asteriacites* have been identified only by the shape of traces and the direction and density of the striations in the arm depressions (e.g. Seilacher, 1953; Hakes, 1976: Twitchett and Wignall, 1996; Wilson and Rigby, 2000; Fourie, 2009; Bernardi and Avanzini, 2011; Ishida *et al*., 2004, 2013). Based on the detailed observations of morphology of the striations in this study, the two ichnospecies of *Asteriacites* were more clearly distinguished. The striations of *Asteriacites lumbricalis* (Figure 8) were fine, parallel to each other, perpendicular to the arm axis, well spaced

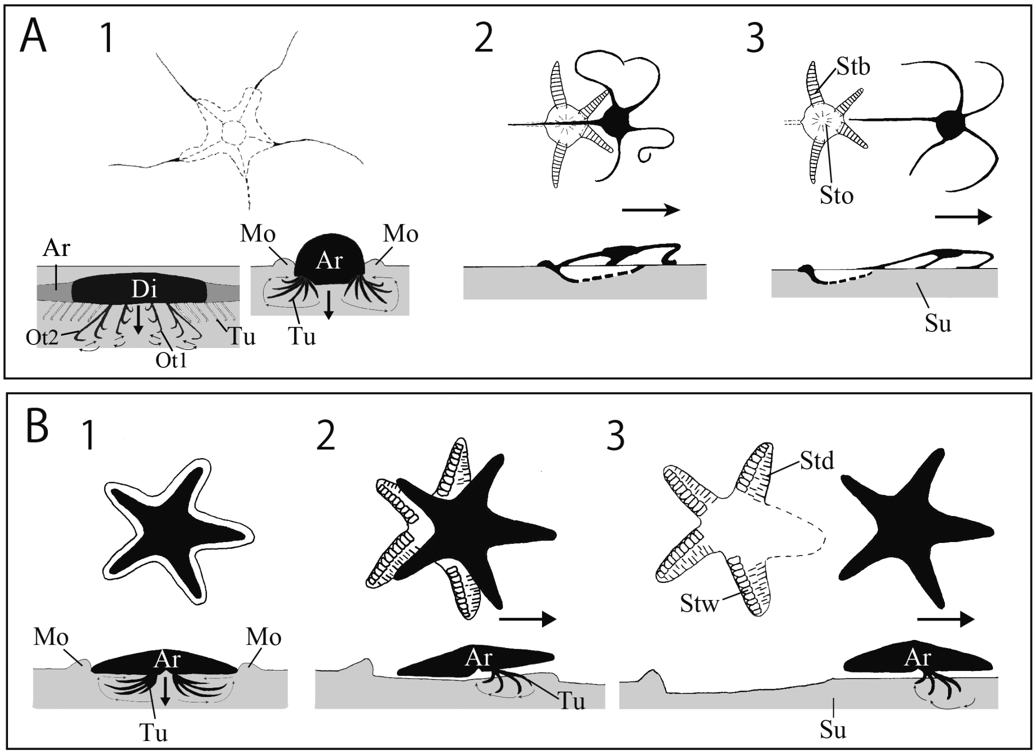

Figure 10. Horizontal and vertical schematic diagrams of the process of production of the striations of *Asteriacites lumbricalis* by ophiuroids in (A) and of *A. quinquefolius* by asteroids in (B). Thin and thick arrows show the movement of tube-feet and the direction of travel of the animals, respectively. Abbreviations: Ar, arm; Di, disc; Mo, mound of substratum; Ot1, first oral tube-foot; Ot2, second oral tube-foot; Stb, striation by basal-arm tube-feet; Std, deep striation; Sto, striation by oral tube-feet; Stw, wide striation; Su, substratum; Tu, tube-foot. Modified from Ishida *et al.* (2004, fig. 4) and Ishida *et al.* (2013, fig. 4).

in the four arm depressions, and fine, radial in the center depression, while those of *A. quinquefolius* (Figure 9) were deep and irregular in the front half of each arm depression, and wide, regular, and in contact in the other half. Furthermore, the analyses of the producing process of the striations by ophiuroids and asteroids in aquariums and *in situ* (Figure 10) clarified that the striations of *A. lumbricalis* and *A. quinquefolius* were produced by the movement of basal-arm tube-feet and oral tube-feet of fossil ophiuroids and of the tube-feet of fossil asteroids, respectively. Consequently, this study unequivocally corroborated that *A. lumbricalis* was, indeed, produced by ophiuroids, and *A. quinquefolius* by asteroids.

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